Impacts of shallow lake restoration on vegetation and breeding birds in Iowa

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Abstract

The Shallow Lakes Restoration Project aims to restore eutrophic shallow lakes throughout the Iowa Prairie Pothole Region (PPR). We compared the vegetation taxa richness and frequency of taxa in three vegetation groups surveyed in 2016 and 2017 across non-restored sites, younger restorations, and older restorations. We also assessed the impact of these groups on numbers of breeding marsh birds. Restored wetlands had between 2.7 (95% CI 2.3, 3.2) and 4.7 (95% CI 3.9, 5.5) more species than non-restored sites among the three vegetation groups. *Typha* sp. was the most abundant emergent species. *Lemna minor* and *Ceratophyllum demersum* were the most abundant floating-leaved and submersed species, respectively. The frequency of submersed aquatic vegetation increased with years since restoration, while floating-leaved vegetation and *Typha* sp. peaked at 7 years post-restoration. The frequency of *Typha* sp. positively influenced Marsh Wrens and Yellow-headed Blackbirds. Water depth negatively affected Marsh Wrens, but water depth positively influenced Yellow-headed Blackbirds. Floating-leaved vegetation positively affected Virginia Rails, while water depth had a negative effect on this species. Our results indicate that after about 7 years further management of the vegetation and water levels may need to occur and should include maintaining appropriate conditions for breeding marsh birds.

KEYWORDS: marsh bird, restoration, wetland vegetation

Introduction

Wetlands in the Prairie Pothole Region (PPR) have experienced dramatic declines and alterations since European settlement (Dahl 2014). This area was once characterized by expansive wetlands interspersed with grasslands and hosted diverse wildlife and floral populations (Bishop 1981, Tiner 1984, Van Meter and Basu 2015). Due to agricultural expansion more than half of the wetland area has been lost in the conterminous United States alone (Dahl 2014). Many of the wetlands that remain have been altered due to watershed changes, increased fish abundance, increased sedimentation, and excess nutrient loading and chemical drift (Martin and Hartman 1986, Neely and Baker 1989, Baker 1992, Euliss and Mushet 1996, Gleason et al. 2003). Wildlife species, including birds, rely on emergent and submersed aquatic plants for nesting and foraging, and the severe decline in quality wetland habitat has likely led to a decline in many species (Banks and Springer 1994, Page and Gill 1994, Igl and Johnson 1997, Lor and Malecki 2002, Anteau and Afton 2008). In response to these changes, wetland restoration that involves manipulating water levels have become important tools for expanding and improving the quality of habitat for a variety of wildlife species, including birds (Rundle and Fredrickson 1981, Elphick and Oring 1998, Taft et al. 2002).

Historically, wetlands in the PPR experienced varying amounts of vegetation and open water over time, which resulted in seasonal or annual changes in the avian community (Weller and Spatcher 1965, Murkin et al. 1997, Hershey et al. 1999, Murkin and Ross 2000). During drought periods, seeds from vegetation germinate and more nutrients become available as plant litter decomposes (Harris and Marshall 1963, van der Valk and Davis 1976, Bärlocher et al. 1978). The basin gradually refills and submersed aquatic, floating-leaved, and emergent vegetation gradually increases (van der Valk and Davis 1978). Emergent vegetation will eventually die back due to prolonged inundation and muskrat activity, and this will lead to an open lake period once again (van der Valk and Davis 1978). During the vegetated periods, the presence of emergent and aquatic vegetation provide favorable conditions for breeding marsh birds. For example, the growth of tall emergent vegetation, such as *Typha* sp. and *Scheonoplectus* sp., can be used as a substrate for nest building by marsh passerines, particularly

Marsh Wrens and Yellow-headed Blackbirds (Kroodsma and Verner 2013, Lupien et al. 2014). Similarly, secretive marsh birds will use *Typha* sp. for nesting, foraging, and displaying (Lor and Malecki 2006, Harms and Dinsmore 2013, Glisson et al. 2015). Submersed aquatic vegetation can be used as a substrate for aquatic invertebrates (Voigts 1976, Driver 1977, Wrubleski 1999, Murkin and Ross 2000), which are important parts of the diets of several marsh passerines and secretive marsh birds (Conway 1995, Twedt and Crawford 1995, Kroodsma and Verner 2013). Floating-leaved vegetation, such as duckweeds, may also provide habitat for invertebrates (Harper and Bolen 1996).

However, agriculture and development have altered water level fluctuations and water quality in remaining wetlands, particularly shallow lakes, which are semi-permanent or permanent wetlands <1 m deep (Cowardin et al. 1979, Miller et al. 2012, Geisthardt et al. 2013). A combination of wetland consolidation and an increase in the abundance of planktivorous and benthivorous fishes contribute to more stable water conditions and increased sedimentation (Peterka 1989, Hanson and Butler 1994, Hanson and Riggs 1995, Euliss and Mushet 1996, Zimmer et al. 2000, Pothoff et al. 2008, Stewart and Downing 2008, McLean et al. 2016). Such factors can lead to increased turbidity and concentrations of nitrogen, phosphorus, and phytoplankton (Hanson and Riggs 1995, Zimmer et al. 2002). Subsequently, submersed aquatic vegetation declines and further allows for increased phytoplankton growth, and the persistent deep water causes emergent vegetation to decline (van der Valk and Davis 1978, Timms and Moss 1984, Scheffer et al. 1993, Sayer et al. 2010). The loss in vegetation and increased turbidity do not provide appropriate habitat for invertebrates (Scheffer et al. 1993, Zimmer et al. 2000) and reduces appropriate foraging and nesting conditions for many breeding birds (Glisson et al. 2015).

In an effort to remedy the degradation of shallow lakes, several restoration projects have focused on implementing the natural wet-dry cycle as a management tool (Chow-Fraser 2005, Giesthardt et al. 2013). Many of these projects focus on maintaining conditions that favor abundant vegetation, particularly emergent vegetation and submersed aquatic plants, and may result in a shift to a clear water state (Scheffer et al. 1993, Chow-Fraser 2005, Søndergaard et al. 2007). Compared to unmanaged wetlands, restored wetlands tend to improve habitat conditions for breeding birds (VanRees-Siewert and Dinsmore 1996, Connor and Gabor 2006, Kaminski et al. 2006). However, several factors may prevent a project from persisting in this desired state for long periods of time (e.g., >10 years), and habitat suitability for marsh birds may actually decline (Glisson et al. 2015). Continuous management, such as water level manipulations and invasive species control, may be necessary (Søndergaard et al. 2007, Hanson et al. 2017). For example, submersed aquatic plants are known to help stabilize the clear water state of shallow lakes (Carpenter and Lodge 1996, Scheffer et al. 1993, Jeppesen et al. 1997), but they may not immediately respond to restoration efforts (Strand 1999, Søndergaard et al. 2007, Bortolotti et al. 2016). Additionally, external nutrient inputs may further prevent the proliferation of submersed aquatic plants (Lauridsen et al. 2003a, Zimmer et al. 2003), so additional management tools may be needed to increase vegetation growth. Monitoring the vegetation community and its impacts on wetland-dependent wildlife may help elucidate when such actions are warranted.

Since 2006 the Iowa Department of Natural Resources and Ducks Unlimited, Inc. have restored over 38 shallow lakes in Iowa PPR through the Shallow Lakes Restoration Project (SLRP). The goal of the SLRP is to improve water quality and the vegetation community to increase the establishment of diverse fish, bird, and invertebrate communities (Geisthardt et al. 2013). Since its implementation, these shallow lakes have shown improvements in water quality and vegetation structure (Geisthardt et al. 2013). However, as they age some shallow lakes appear to be showing a decline in water and vegetation cover (Geisthardt et al. 2013), indicating a need for further management. Our goals were to record the vegetation community of these shallow lakes, determine how they change over time by collecting information from shallow lakes of various states (i.e., years since restoration), and examine how the vegetation affects numbers of wetland-dependent birds. We expected restored shallow lakes to have a greater species richness and frequency of emergent and aquatic vegetation. At the same time, we expected some vegetation (e.g., *Typha* sp., submersed aquatic vegetation) to decline with years since restoration. We also hypothesized that several taxa would influence the abundance of secretive marsh birds. Because they provide nesting substrates and habitat for prey items, we expected emergent vegetation, floating-leaved vegetation, and submersed aquatic vegetation to have positive effects on marsh birds (Verner 1965, Verner and Engelsen 1970, Lor and Malecki 2006, Harms and Dinsmore 2013). Additionally, we hypothesized that the general height and density of vegetation and water depth may influence the counts of marsh birds (Verner 1965, Sayre and Rundle 1984, Twedt and Crawford 1995, Tozer et al. 2010, Lupien et al. 2014).

Methods

Study Area

Our study shallow lakes were located within the Des Moines Lobe region in Iowa, an area formed by the retreating Wisconsin glacial advance 14,000 years ago (IAN 2001, Miller et al. 2009). The PPR covers about 700,000 km^2 in the United States and Canada, and the DML makes up only 800 km^2 of that area (Bishop et al. 1981, Kantrud et al. 1989, IAN 2001, Dahl 2014). The PPR is characterized by palustrine and lacustrine wetlands (Kantrud et al. 1989).

In this study, the term "restored" refers to shallow lakes that were once severely degraded and subsequently restored by manipulating the hydrology to improve water quality and vegetation. These shallow lakes were passively restored (i.e., no seed additions), and they were drained using an existing outlet structure to begin the restoration process. Infrastructure, such as water control structures, water channels, pipelines, and fish exclusion structures, were installed into nearly all shallow lakes to manage water levels and exclude rough fish. However, some sites still contained rough fish during the survey periods. Once the restoration process began, sites were refilled gradually over (ideally) a 2-year period to allow vegetation to reestablish. Likewise, the term "non-restored" refers to shallow lakes that were unmanipulated. Most of these shallow lakes were void of emergent vegetation and contained turbid water; some may be restored within the next few years. We considered the date of restoration to be the start of the drawdown, even if it was before completion of the water control structure. The years since restoration ranged between 1 and 12 years, but most restored shallow lakes were restored >2 years prior to this study.

Site Selection

To examine how shallow lakes in different restoration states differ in vegetation composition and influence breeding bird use, 19 restored sites were chosen based on years since restoration, spanning the period from one to eleven years post-restoration. Because only about 38 shallow lakes had been restored at the start of this study, we had a limited number of restorations to choose from. We wanted to survey at least two shallow lakes at each "age". We randomly chose shallow lakes in each age class, but we could not do this for every age group, as there was often only one. Based on recommendation from the Iowa DNR, we also chose 11 non-restored shallow lakes to examine pre-restoration bird use of shallow lakes. One of these shallow lakes was in the early stages of restoration in 2017 and, therefore, considered to be a restored site in that year. Study sites were located in 12 Iowa counties: Buena Vista, Calhoun, Cerro Gordo, Clay, Dickinson, Emmet, Hancock, Palo Alto, Pocahontas, Winnebago, Worth, and Wright. All shallow lakes were surveyed in the summer of 2016 and 2017.

We grouped restored shallow lakes into two categories based on years since restoration for some of the analyses. Several studies have examined the changes in the vegetation community of restored sites at different ages (Galatowitsch and van der Valk 1996a, b, Aronson and Galatowitsch 2008), and others have found that sites considered to be "older" may differ from "younger" sites (Badiou et al. 2011, Bortolotti et al. 2016). For example, previously degraded wetlands restored 1-3 years prior to the study by Bortolotti et al. (2016) had less submersed aquatic vegetation (SAV) indicative of remnant (i.e., undisturbed) wetlands compared to wetlands restored 7-10 years prior. Additionally, Søndergaard et al. (2007) determined that 5-10 years after biomanipulation some shallow lakes returned to a eutrophic, turbid state with little to no vegetation. Based on these findings we examined our sites using the following grouping method (hereafter referred to as restoration state): non-restored, younger (1-5 years since restoration), and older (6-11 years since restoration). This grouping method provided a more balanced design, and we were particularly interested in whether these restorations were showing signs of returning to aa eutrophic state >5 years post-restoration.

Vegetation Sampling

We completed vegetation surveys once during each of the two summers in 2016 and 2017. We used a method similar to Webb et al. (2010) and created north-south and east-west transects in each shallow lake. These were situated along the maximum width of each shallow lake for each direction. We used a 1 x 1 m quadrat every 50 m for transects ≤800 m and every

100 m for transects >800 m (Webb et al. 2010). These transects were generated using ArcMap 10.3 (Environmental Systems Research Institute, Inc., Redlands, CA). At each quadrat we recorded the percent cover of plants to genus (e.g., *Typha* sp.; Monfils et al. 2014) or species and their structural definition (wet prairie, sedge meadow, shallow emergent, deep emergent, submersed aquatic, floating-leaved, mudflat annual, and woody shrub; Galatowitsch and van der Valk 1994). For all groups other than submersed aquatics and floating-leaved plants percent cover was calculated using basal cover. We estimated the areal percent cover of submersed aquatics and floating-leaved plants. We used a rake to facilitate the identification of submersed aquatic plants. We assigned each quadrat into one of three size classes based on maximum vegetation height (1 = 0 – 0.5 m, 2 = 0.5 – 1 m, 3 = >1 m; Harms and Dinsmore 2013). We used a similar method for vegetation density and assigned each quadrat into one of three density classes (1 = completely open, 2 = anything that falls in between the two extremes, 3 = water not visible through the base of stems at water level; Conway 2009). Water depth was recorded to the nearest cm at the center of each quadrat.

Bird Surveys

We conducted unlimited-radius, 10-min point counts throughout each site for breeding marsh birds (Ralph et al. 1995). Points were situated randomly in shallow lakes, and the number of points depended on the size of the site. Two points were placed in sites 10.1 – 20 ha, three points in sites 20.1 – 30 ha, four points in sites 20.1 – 40 ha, and five points in sites >40 ha (Harms 2011). Points were situated >400 m apart to avoid double-counting individual birds (Conway 2011). We surveyed each set of points twice during each year to account for any seasonal variation in the vocalization rates of species (Gibbs and Melvin 1993, Conway et al.

2004). Point counts were conducted between a half-hour before sunrise to up to four hours after sunrise. We did not survey in rainy conditions or when winds exceeded 20 km/h (Conway 2009).

To improve detection of secretive marsh birds (i.e., rails, bitterns, grebes), we incorporated call-broadcast surveys into our point count surveys according to methods described by the North American Marsh Bird Monitoring Protocol (Conway 2009, 2011). The first five minutes of the survey period were silent, while the last five minutes were recorded calls. Each minute corresponded to one of five species of secretive marsh birds; the first 30 sec included a recording, followed by 30 sec of silence. The sequence of calls we used, from first to last, was Least Bittern (*Ixobrychus exilis*), Sora (*Porzana carolina*), Virginia Rail (*Rallus limicola*), King Rail (*Rallus elegans*), and Pied-billed Grebe (*Podilymbus podiceps*; Conway 2011). Except for the King Rail, these are regular breeders in Iowa. In previous call-broadcast surveys conducted in Iowa (Harms 2011), the King Rail did not have many detections, but Sora and Virginia Rail tended to respond to King Rail calls as readily as they responded to intraspecific calls (T. Harms, pers. comm.). We used an MP3 player (SanDisk Sansa Clip 1GB, SanDisk Corporation, Milpitas, California) attached to portable speakers (JBL Flip 3, Harman International Industries, Inc., Stamford, Connecticut) and broadcast at 90 dB from a distance of 1 m in front of the speakers (Conway 2011). The speaker faced the interior of the wetland and was 0.5 m from the ground or water surface (Harms 2011). Because we conducted surveys twice per year, we averaged the number of birds counted between the two visits for each year.

Vegetation Community Analysis

We examined the community structure of three major functional groups of plants (Galatowitsch and van der Valk 1994): emergent vegetation, submersed aquatics, and floating-leaved vegetation. We mostly encountered deep emergent and shallow emergent species and the other functional groups alone were not encountered enough for statistical analyses. We were interested in how several measurements of these groups differed across shallow lakes in different restoration states. Since our study unit was the shallow lake, we averaged the following metrics across the three restoration states: total taxa richness and frequency of occurrence for each taxa. We decided to average most of our calculations across sites ($n = 60$) because these data tended to be zero-inflated at the quadrat level ($n = 1,472$). We examined total taxa richness within each of three plant functional groups. We used taxa richness because we included both species and plants identified to genus. Frequency of occurrence is the percentage of points each taxa was encountered at a shallow lake. Because these metrics were non-normal and tended to have unequal variances across the restoration states, we used a Kruskal-Wallis rank sum test to examine differences in taxa richness and frequency of occurrence among restoration states (Kruskal and Wallis 1952). We did not find an effect of year for all metrics, so we combined data across both years. For significant ($P < 0.05$) differences we used a Games-Howell multiple comparisons test to determine which restoration states were different (Games and Howell 1976).

We were also interested in how frequency and percent cover changed with years since restoration and water depth, respectively. For a subset of these taxa, we used two different methods to examine the response of plant taxa to years since restoration and water depth. We assessed years since restoration and water depth separately because we were interested in the separate effects of each covariate on changes in taxa frequency or water depth. Furthermore, frequency of occurrence was a site-level metric, while water depth was measured at the quadrat level. For years since restoration, we used a linear mixed effects models (*lme4* package in R; Bates et al. 2015), with frequency as the response variable and a linear or quadratic effect of years since restoration as the explanatory variable. We also included year as a fixed effect and site as a random effect to account for the repeated measures of frequency at each shallow lake (Zuur et al. 2009). We used a likelihood ratio test to determine the most competitive model (linear vs. quadratic). We had an adequate number of encounters for the following 10 taxa to assess years since restoration: *Bulboschoenus fluviatilis, Phalaris arundinacea, Phragmites australis*, *Schoenoplectus sp.*, *Typha sp.*, total floating-leaved vegetation, *Ceratophyllum demersum*, *Potamogeton sp.*, *Stuckenia pectinata,* and *Urticularia vulgaris*, and total submersed aquatic vegetation. We decided to examine only floating-leaved vegetation because these species showed similar patterns in occurrence among restoration states, and several species had no occurrences at non-restored sites. Because these were frequencies, we transformed them using the arcsine-square root function (Zar 2010). For these same groups we examined Pearson's correlation coefficients between percent cover of each plant taxa and water depth.

Vegetation Effects on Marsh Bird Abundance

We were interested in the relationship between several vegetation variables and counts of breeding birds. Specifically, we made several hypotheses concerning the directional effects of vegetation variables and water depth on two groups and three species of birds (Table 1). Marsh passerines included four species of obligate wetland breeding passerines (Brown and Smith 1998): Marsh Wren (*Cistothorus palustris*), Swamp Sparrow (*Melospiza georgiana*), Red-winged Blackbird (*Agelaius phoenicus*), and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). Secretive marsh birds included American Bittern (*Botaurus lentiginosus*), Least Bittern, Virginia Rail, and Common Gallinule (*Gallinula galeata*). We assessed these groups because they require emergent vegetation for nesting and foraging (Lor and Malecki 2006, Tozer et al. 2010, Kroodsma and Verner 2013). There is also evidence that they are sensitive to certain habitat conditions, such as water quality, and so may be considered wetland quality indicators (Eddleman et al. 1988, Conway 1995, Cumbee et al. 2008, Lowther et al. 2009, Glisson et al. 2015). Additionally, we examined the effect of vegetation and water depth on Marsh Wren, Yellow-headed Blackbird, and Virginia Rail separately; these are relatively common species in Iowa wetlands but are experiencing population declines elsewhere (Conway et al. 1994, Conway 1995, Kroodsma and Verner 2013).

We used linear mixed models to assess the effect of these habitat variables on breeding birds (*lme4* package in R; Bates et al. 2015). We always included year as a fixed effect and site as a random effect to account for any inter-year variation and the repeated measures conducted on wetlands (Zuur et al. 2009). We generated a global model for each group and species, and avoided including variables with a VIF > 5 in the same global model (Montgomery and Peck 1992). We square root transformed any variables that did not meet assumptions of normality and homogeneity (Zar 2010). We used backward elimination of the fixed effects to determine the final model (*lmerTest* package in R; Kuznetsova et al. 2017).

Results

We surveyed a total of 742 quadrats between 5 July and 21 August in 2016 and 730 quadrats between 27 June and 12 August in 2016 at 30 shallow lakes. The number of quadrats in each restoration state was relatively similar, but we had fewer quadrats in older restorations (Table 2).

Species richness differed among restoration states for emergent ($\chi^2_2 = 33.53$, $P < 0.01$), floating-leaved ($\chi^2_2 = 65.63$, $P < 0.01$), and submersed aquatic vegetation ($\chi^2_2 = 26.24$, $P < 0.01$; Fig. 1A). For emergent species, both older ($t_{47} = 4.10$, $P < 0.01$) and younger ($t_{69} = 6.90$, $P < 0.01$) restorations had more species than non-restored sites. There were also more floating-leaved species at older ($t_{45} = 10.60$, $P < 0.01$) and younger ($t_{65} = 9.50$, $P < 0.01$) restorations than at non-restored shallow lakes. Similarly, there were more species of submersed aquatic vegetation at older ($t_{72} = 4.27$, $P < 0.01$) and younger ($t_{82} = 4.71$, $P < 0.01$) restorations.

Frequency of occurrence for species differed for some emergent and floating-leaved vegetation across restoration states (Table 3; Fig. 1). Among emergent species, *Typha* sp. was encountered more frequently than any other species for both younger and older restorations ($\chi^2_2 = 33.18$, $P < 0.01$; Fig. 1B). *Typha* sp. had a greater frequency at older and younger restorations than non-restored shallow lakes. For other emergent species, frequency tended to be greater at restored sites than non-restored sites, but this pattern was not significant. Of the floating-leaved species, *Lemna minor* ($\chi^2_2 = 29.95$, $P < 0.01$), *Lemna trisulca* ($\chi^2_2 = 13.47$, $P < 0.01$), *Spirodela polyrhiza* ($\chi^2_2 = 17.51$, $P < 0.01$), and *Wolffia* sp ($\chi^2_2 = 20.05$, $P < 0.01$) differed among the restoration states (Fig. 1C). Both *Lemna minor* and *Spirodela polyrhiza* had greater frequencies in older and younger restorations than non-restored sites. *Wolffia* sp and *Lemna trisulca* had greater frequencies in older restorations than non-restored sites. Although non-restored sites and younger restorations tended to have greater frequencies of submersed aquatic vegetation, this relationship was not significant (Fig. 1D).

Years since restoration influenced the frequency of three species and two functional groups, and water depth showed a significant correlation with percent cover of some taxa. *Typha* sp., floating-leaved vegetation, and *Urticularia vulgaris* increased and then decreased with years since restoration (7-year peak) (Fig. 2B). Submersed aquatic vegetation and *Ceratophyllum demersum* showed a positive linear relationship with years since restoration (Fig. 2A). Three emergent species showed a significant negative relationship with water depth, while all the floating-leaved and submersed aquatic vegetation groups showed a strong positive relationship with water depth (Table 4).

Five habitat variables influenced counts of breeding marsh birds (Table 5). The final model for marsh passerines included a positive effect of *Typha* sp., and a positive effect of submersed aquatic vegetation. *Typha* sp. positively influenced numbers of Marsh Wrens, while *Typha* sp., submersed aquatic vegetation, and water depth all positively influenced numbers of Yellow-headed Blackbirds. The secretive marsh bird final model included a positive effect of floating-leaved vegetation, and a positive effect of moderately dense vegetation. Floating-leaved vegetation positively influenced and water depth negatively influenced counts of Virginia Rails.

Discussion

Restored shallow lakes in the Iowa PPR are showing changes in the vegetation community after restoration, and we found evidence that some of these vegetation changes may influence breeding marsh birds. Within a few years post-restoration, a variety of emergent, floating-leaved, and submersed aquatic vegetation created a more species rich-community, and these vegetation groups showed positive effects on both marsh passerines and secretive marsh birds. However, the frequency of different plant taxa was highly variable among years and restoration states. This is likely due to the timing of the drawdown and the reflooding periods of restoration, when nutrients become available and facilitate vegetation growth (Kadlec et al. 2000, van der Valk 2000). At the same time, we found that parts of the vegetation community are beginning to decline with time since restoration, which may have important implications for management decisions concerning marsh birds. These declines may be a result of prolonged inundation (van der Valk and Davis 1978), increases in planktivorous fishes (Timms and Moss 1984, Jeppesen et al. 1997, Zimmer et al. 2001), sedimentation (Jurik et al. 1994, Euliss and Mushet 1996), or increased nutrient loading from the surrounding landscape (Neely and Baker 1989, Lauridsen et al. 2003b).

Overall, restorations are showing increases in taxa richness and frequency of occurrence of vegetation as they progress, but these factors may be declining in older restorations. In particular, we found that younger restorations tended to have more species in the emergent group. This influx of productivity within the first few years of restoration results from exposing the wetland soil, encouraging the germination of seeds already in the seed bank (van der Valk and Davis 1976, Wienhold and van der Valk 1989). Seeds may also be dispersed from nearby wetlands or ditches (Kettenring and Galatowitsch 2011) or from waterbirds (Figuerola et al. 2002). However, the seeds of some species vary in their ability to remain viable after several years of inundation prior to restoration (Wienhold and Galatowitsch 1988) and others may not be so easily dispersed (Kettenring and Galatowitsch 2011). Invasive perennials, such as *Phalaris arundinacea* and *Typha* x *glauca,* can also dominate initial restoration efforts, outcompeting and preventing the establishment of native plants (Aronson and Galatowitsch 2008, Mitchell et al. 2011, Lishawa et al. 2013). This could explain the lower species richness of older restorations; *Typha* sp. was the most frequently encountered emergent species and had the greatest overall frequency in both older and younger restorations. At the same time, *Typha* sp. showed a quadratic relationship with years since restoration and peaked in frequency at around 7-8 years after restoration. This may be due to muskrat activity (pers. obs.) and prolonged inundation (van der Valk and Davis 1978). Indeed, we found that *Typha* sp. showed a negative correlation with water depth.

Floating-leaved and submersed aquatic species also appear to be increasing in frequency, and these species are particularly important in stabilizing the clear water state of restored shallow lakes and providing habitat and forage for wildlife (Carpenter and Lodge 1986, Jeppesen et al. 1997, Lumsden et al. 2015). Total frequency of floating-leaved vegetation appeared to peak within 5 to 6 years after restoration. Species such as *Lemna minor*, *Spirodela polyrhiza*, and *Wolffia* sp. tended to have their greatest frequencies in older restorations, but these were not significantly greater than younger restorations. This variation and decline could be due to grazing from waterfowl (Lauridsen et al. 1993), water level fluctuations (Chow-Fraser 2005), changes in light conditions (Bini et al. 1999), temperature (Minc 1997, Smith and Moelyowati 1998), or changes in nutrient inputs (Lougheed et al. 2001). Floating-leaved vegetation also showed a relationship with years since restoration that was similar to emergent cover. Along with several emergent species, the abundance of floating-leaved species may be driven by high nutrient content (e.g., phosphorous), so perhaps the similarities between the two functional groups are due to changes in the water chemistry (Bini et al. 1999).

In contrast, submersed aquatic species may not have reached their peak in these restorations. There is evidence that submersed aquatic vegetation growth can be delayed in shallow lake restorations (Lauridsen et al. 1994, Søndergaard et al. 2007, Bortolotti et al. 2016) and species composition changes over time (Hansel-Welch et al. 2002) and with sediment type (Lauridsen et al. 1994). However, some species are less tolerant of changes in water condition (e.g., underwater light availability), and the most frequently encountered submersed aquatic vegetation in this study appeared to be species that can tolerate a range of conditions. *Ceratophyllum demersum* and *Stuckenia pectinata* were the most abundant submersed aquatics. These species tend to be more tolerant of slightly turbid waters, partly because each species is structurally adapted to survive in low-light conditions (Bini 1999, Lougheed et al. 2001). *Ceratophyllum demersum* forms dense canopies beneath the water surface, while *Stuckenia pectinata* has leaves that float on or just below the water’s surface (Lougheed et al. 2001). They were also present in several non-restored sites. On the other hand, *Urticularia vulgaris, Najas* sp., and some species of *Potamogeton* (e.g., *Potamogeon foliosus*) have smaller leaves that do not reach the surface, so they are more sensitive to low light availability (Lougheed et al. 2001). These taxa were less abundant in non-restored sites, and *Urticularia vulgaris* showed a quadratic relationship with years since restoration. This, along with the changes in floating-leaved vegetation, may indicate that these sites could revert to a eutrophic, turbid state.

Changes in the macrophyte structure and composition have the potential to influence avian communities in prairie wetlands (Fairbairn and Dinsmore 2001, Rehm and Baldassarre 2007, Harms and Dinsmore 2013), and we found this to be consistent in our study sites. Importance of emergent vegetation, particularly *Typha* sp., was evident for almost all of our focal groups and species. The positive relationship between *Typha* sp. and counts of breeding marsh birds has been found by other studies and in other regions of North America (Tozer et al. 2010, Harms and Dinsmore 2013, Lupien et al. 2014). In particular, the robust leaves of *Typha* sp. provide an appropriate surface for nest building by breeding marsh passerines (Twedt and Crawford 1995, Mowbray 1997, Kroodsma and Verner 2013). Both Marsh Wrens and Yellow-headed Blackbirds use emergent vegetation as a surface on which to build their nests (Verner 1965, Willson 1966). Marsh Wrens primarily used *Typha* sp. in these shallow lakes, although they may use other dominant robust emergent species such as *Schoenoplectus* sp. if there is standing water (Verner 1965, Verner and Engelsen 1970).

Along with *Typha* sp., we found that water depth influenced numbers of Marsh Wrens and Yellow-headed Blackbirds. Both species commonly build nests over deep water (Willson 1966, Minock and Watson 1983, Twedt and Crawford 1995), and we found that water depth had a significant positive effect on Yellow-headed Blackbird numbers. On the other hand, Marsh Wrens showed a negative relationship with water depth. Other studies have found a positive trend between water depth and Marsh Wren abundance or occupancy (Tozer et al. 2010, Lupien et al. 2014). However, unlike these studies, Yellow-headed Blackbirds were common breeders and tended to occur in the same sites as Marsh Wrens in our study area. Both species are aggressive territory defenders and Yellow-headed Blackbirds are known to exclude Marsh Wrens from their territories (Bump 1986, Harms and Dinsmore 2015). In this case, it could be that Yellow-headed Blackbirds exclude Marsh Wrens from areas with deeper water.

We expected secretive marsh birds and Virginia Rails to be influenced by frequency of *Typha* sp., but we found that secretive marsh birds were positively influenced by the amount of moderately dense vegetation. Virginia Rails did not show any significant relationship with emergent vegetation characteristics. Overall vegetation structure and water conditions may be more important than emergent species composition for this group and species (Rundle and Fredrickson 1981). Robust and dense stands of emergent vegetation can provide appropriate habitat conditions for several species of secretive marsh birds (Lor and Malecki 2006, Tozer et al. 2010, Harms and Dinsmore 2013). Several species, including Least Bitterns and Virginia Rails, will build their nests at the base of emergent vegetation and may use the leaves as a canopy (Weller 1961, Conway 1995). At the same time, some degree of interspersion between vegetation and water tends to provide appropriate nesting conditions for a greater variety of secretive marsh birds (Weller and Spatcher 1965, Lor and Malecki 2006), which might explain the importance of moderately dense vegetation. On the other hand, water depth was a more important factor for Virginia Rails, which showed a negative relationship with water depth. Virginia Rails generally use and nest in areas with shallow water (< 20 cm; Rundle and Fredrickson 1981, Sayre and Rundle 1984, Lor and Malecki 2006). Indeed, we found that Virginia Rails had a negative relationship with water depth.

Along with emergent vegetation, submersed and floating aquatic species appeared to be important for some groups. Both marsh passerines and Yellow-headed Blackbirds showed a positive relationship with frequency of submersed aquatic vegetation. This vegetation can provide habitat for a variety of macroinvertebrates (Krull 1970, Voigts 1976, Driver 1977, Hanson and Butler 1994), which are important in the diets of breeding marsh birds (Twedt and Crawford 1995). Yellow-headed Blackbirds and Marsh Wrens will forage on emerging aquatic insects at the water's surface (Twedt and Crawford 1995, Kroodsma and Verner 2013). These and other breeding marsh birds will also nest over deep water, which can provide appropriate conditions for submersed aquatic vegetation (Sheldon and Boylen 1977). Indeed, some studies have found a positive relationship between the abundance of these species and water depth (Tozer et al. 2010). Similarly, floating-leaved vegetation can also provide habitat for macroinvertebrates (Harper and Bolen 1996), which may also explain this variable's relationship with Virginia Rails. Furthermore, Virginia Rails may use the dense mats of floating-leaved vegetation as a walking surface (Conway 1995).

Management Implications

Our results showed notable differences among the vegetation communities of shallow lakes in different restoration states, which are likely impacting numbers of breeding marsh birds. Because most of our study sites are isolated and exist in a matrix of cropland, they still face pressures from sedimentation, increased nutrient loading, and altered water regimes (Neely and Baker 1989, Anteau 2012, Mushet et al. 2015, Van Meter and Basu 2015). Implementing drawdowns or periodically lowering water levels may be effective management tools for maintaining some years of clear water and abundant submersed aquatic vegetation (Scheffer 1998, Søndergaard et al. 2007). Based on our findings a drawdown every 7 years may be a way to reset the wetland, but further research on restored shallow lakes >7 years of age may be necessary to confirm this timeframe. To increase vegetation species richness, active seeding during drawdown and active removal may prevent monocultures of *Typha* sp. or *Phalaris arundinacea*, particularly in wet prairie or sedge meadow areas (Green and Galatowitsch 2001, Galatowitsch 2006, Lishawa et al. 2010). At the same time, these vegetation changes due to restoration are likely affecting marsh bird abundance. We realize that specific habitat requirements for species in the marsh passerine and secretive marsh bird group are known to differ (e.g., Harms and Dinsmore 2013), but our results may offer some broad implications for improving habitat for the marsh bird community. *Typha* sp. was especially important to several marsh birds, as this emergent species provides shelter and nesting habtiat. At the same time, frequency of submersed aquatic and floating-leaved vegetation also positively influenced marsh bird numbers. Thus, with such large wetlands, maintaining areas with dense emergent cover interspersed with submersed and floating plants will likely provide the greatest variety of habitat types for several species. Furthermore, managing water levels may be necessary to provide a variety of nesting habitats, as water level showed different affects for Yellow-headed Blackbirds and Virginia Rails.

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Figure 1. (A) Mean taxa richness of three vegetation types and mean frequency of (B) emergent, (C) floating-leaved, and (D) submersed aquatic vegetation types for shallow lakes surveyed in the Iowa PPR, 2016 and 2017.

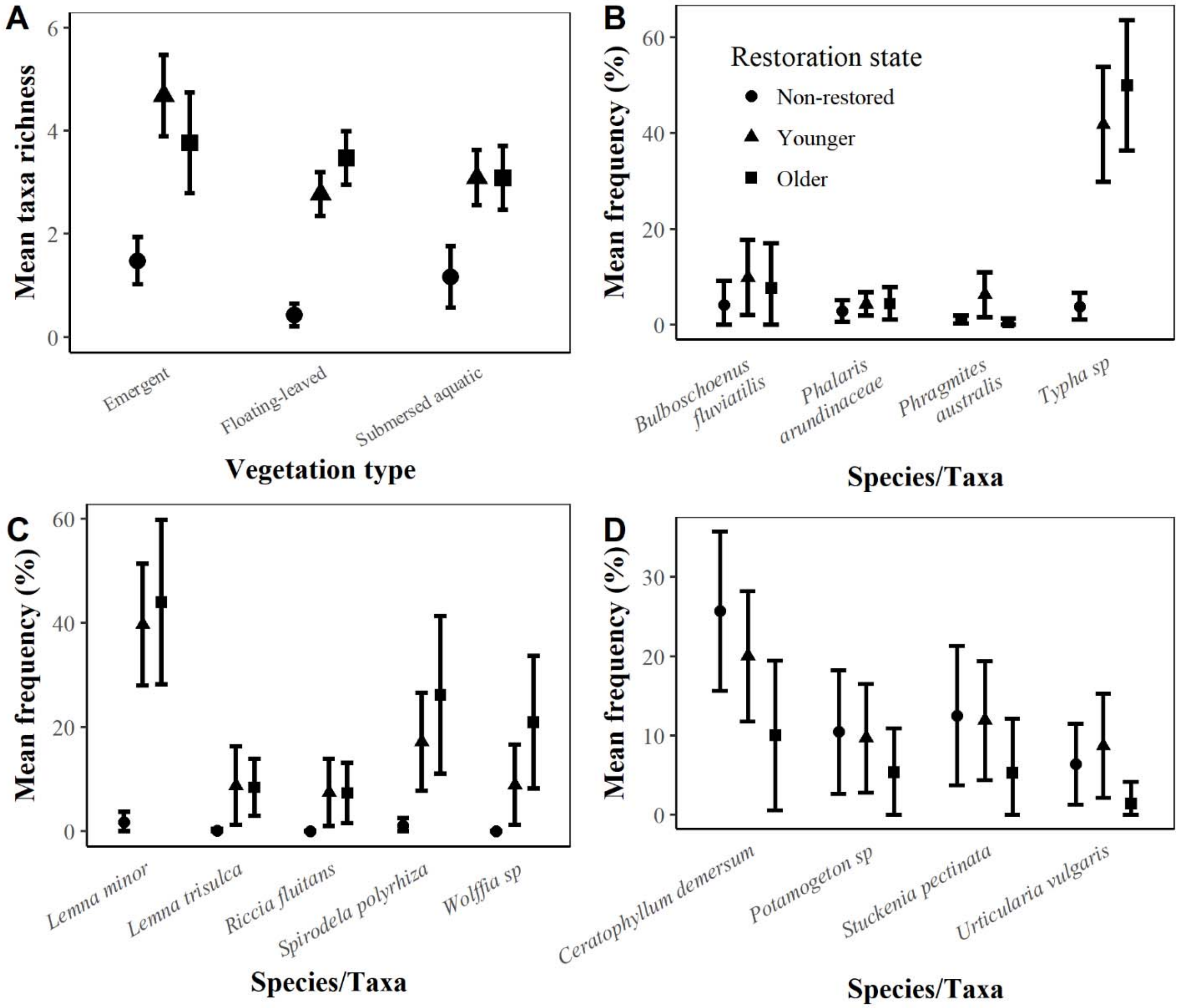

Figure 2. (A) Predicted frequency of *Ceratophyllum demersum* and submersed aquatic vegetation and (B) predicted frequency of *Typha* sp., *Urticularia vulgaris*, and floating-leaved vegetation at shallow lakes surveyed in the Iowa PPR, 2016 and 2017.

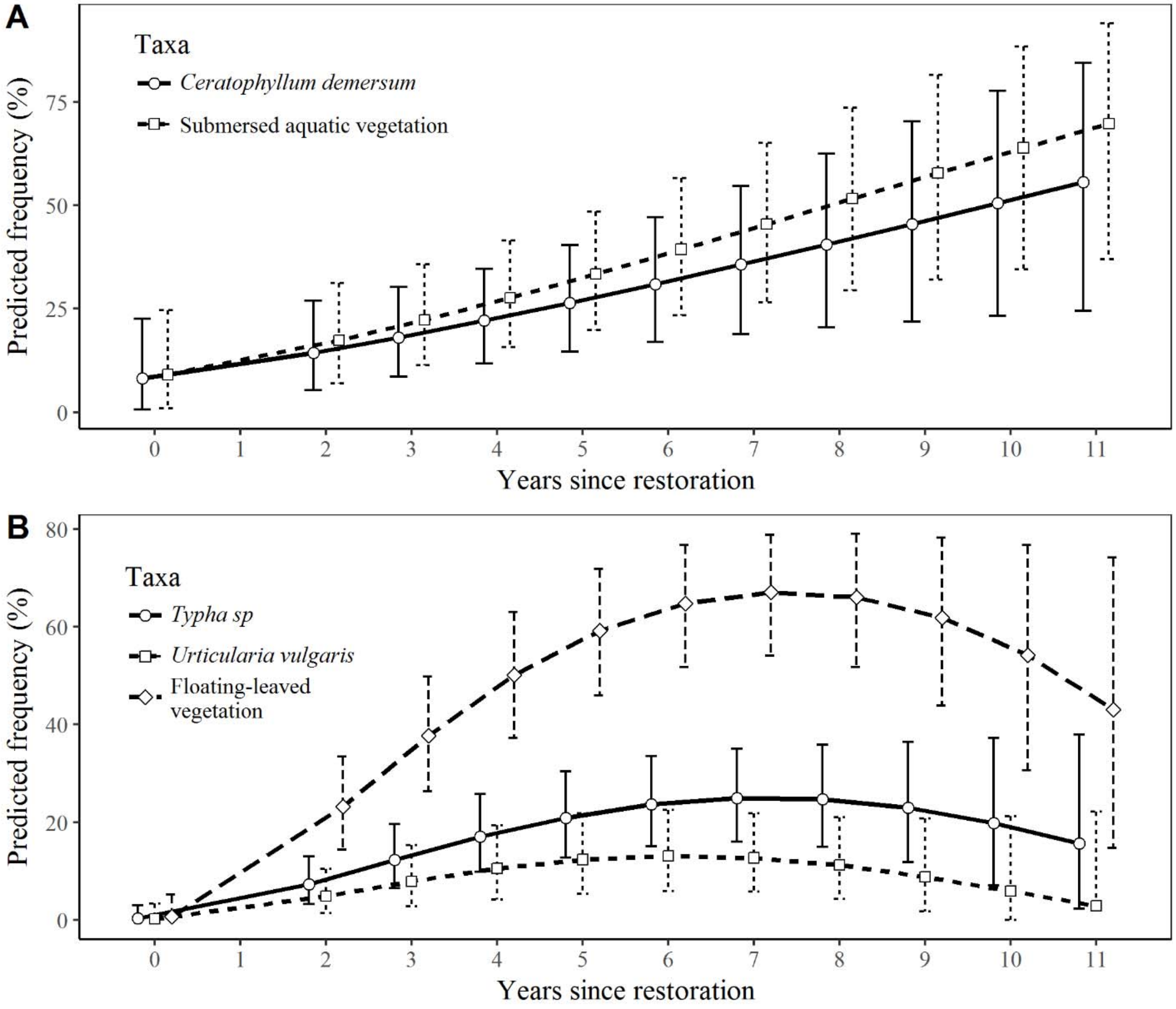

Table 1. Predicted effects of habitat covariates on breeding marsh birds surveyed in the PPR of Iowa, summers 2016 and 2017. We used "+" to represent a positive effect and "-" to represent a negative effect. The variables with "0" were not included in the global models.

Habitat variable	Marsh passerines	Secretive marsh birds	Marsh Wren	Yellow-headed Blackbird	Virginia Rail
Schoenoplectus sp.	0	0	+	0	0
Typha sp.	+	+	+	+	+
Submersed aquatic vegetation	+	+	+	+	+
Floating-leaved vegetation	0	+	0	0	+
Medium vegetation (0.5 – 1 m)	0	+	+	-	+
Highly dense vegetation	+	+	+	+	+
Water Depth (cm)	+	-	+	+	-

Table 2. Number of shallow lakes, number of surveyed quadrats, and mean values (with SD) for years since restoration, area, water depth, marsh passerines, Marsh Wrens, Yellow-headed Blackbird, secretive marsh birds, and Virginia Rails for 30 shallow lakes in the Iowa PPR, summers 2016 and 2017.

	Non-restored	Younger restorations	Older restorations
No. visits	21	17	22
No. surveyed quadrats	504	569	399
Years since restoration	-	4.14 (0.89)	8.12 (1.64)
Area (ha)	116.87 (107.62)	165.53 (173.65)	138.24 (116.48)
Water depth (cm)	115.64 (55.58)	86.96 (42.70)	83.38 (49.95)
Marsh passerines	12.26 (7.18)	27.55 (10.24)	36.21 (12.94)
Marsh Wrens	3.21 (2.60)	9.20 (6.48)	10.91 (4.36)
Yellow-headed Blackbirds	1.76 (2.06)	7.55 (8.86)	12.15 (5.04)
Secretive marsh birds	0.57 (0.80)	2.23 (2.06)	4.06 (3.28)
Virginia Rails	0.40 (0.58)	1.18 (2.09)	2.09 (1.62)

Table 3. Summary of Games-Howell multiple comparisons tests for vegetation taxa that differed in frequency of occurrence among three restoration states of shallow lakes surveyed in the Iowa PPR, summers 2016 and 2017.

Species/Group	Older:Non-restored				Younger:Non-restored				Younger:Older			
	Estimate	t	df	P	Estimate	t	df	P	Estimate	t	df	P
Typha sp.	0.46	6.51	17	< 0.01	0.38	6.03	23	< 0.01	-0.08	0.88	35	0.66
Lemna minor	0.42	5.19	16	< 0.01	0.38	6.26	22	< 0.01	-0.04	0.43	31	0.90
Lemna trisulca	0.08	2.98	16	0.02	0.09	2.25	21	0.09	0.003	0.07	36	1.00
Spirodela polyrhiza	0.25	3.20	16	0.01	0.16	3.3	22	0.01	-0.09	1.00	28	0.59
Wolffia sp	0.21	3.20	16	0.01	0.09	2.3	21	0.08	-0.12	1.60	27	0.27

Table 4. Pearson’s correlation coefficients calculated between percent cover of plant taxa and water depth measured at shallow lakes in the Iowa PPR, summers 2016 and 2017. The asterisks (*) indicate a significant ($P < 0.05$) correlation value.

Taxa	Water depth (cm)
Bulboschoenus fluviatilis	0.02
Phalaris arundinaceae	-0.16*
Phragmites australis	-0.11*
Schoenoplectus sp	0.003
Typha sp	-0.10*
Ceratophyllum demersum	0.36*
Potamogeton sp	0.16*
Stuckenia pectinata	0.21*
Urticularia vulgaris	0.17*
Total submersed aquatic vegetation	0.49*
Total floating-leaved vegetation	0.30*

Table 5. Coefficient estimates (with SE) for vegetation variables by average counts of breeding marsh passerines, secretive marsh birds, and three species of common, obligate, wetland breeders surveyed in the PPR of Iowa, summers 2016 and 2017. The NA represents both variables that were initially in the global model but not included in the final model and variables not considered in the global model. Significant (P < 0.05) effects are indicated with an asterisk (*).

Habitat variable	Typha sp	Submersed aquatic vegetation	Floating-leaved vegetation	Moderately dense vegetation	Water Depth (cm)
Marsh passerines	*2.82 (0.54)	*0.74 (0.35)	NA	NA	NA
Secretive marsh birds	NA	NA	NA	*2.37 (0.50)	NA
Marsh Wren	*1.72 (0.53)	NA	NA	NA	*-0.42 (0.15)
Yellow-headed Blackbird	*2.63 (0.55)	*1.47 (0.32)	NA	NA	*0.40 (0.16)
Virginia Rail	NA	NA	*0.55 (0.23)	NA	*-0.19 (0.11)